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Pleistocene micromammals from Wonderwerk Cave, South Africa: practical issues

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Abstract

The combination of large samples and broken material raises practical issues and potential problems that may be undetectable in smaller samples. Informal identification keys are provided to indicate the types of non-dental features that may be usefully employed when standard features are not present. This process has so far been taken to the generic level. The ratio of minimum numbers of individuals based on mandibles alone (MD) to those obtained using mandibles and maxillae (MNI) varies from 0.59 in Gerbillinae to 0.97 in Macroscelididae, thereby demonstrating that counting only mandibles will skew sample structure. Differential difficulty of identification at lower taxonomic levels, combined with differential susceptibility to breakage, also influences the likelihood that the proportional representation of taxa will be correct.
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Keywords: Pleistocene; Micromammals; Identification; MNIs

1. Introduction

As early as 1941 Malan and Cooke were able to state that Wonderwerk Cave (27° 50′ 45″S: 23° 33′ 19″E), some 45 km south of Kuruman in what is now the Northern Cape Province of South Africa, 'has long been known as a site at which prehistoric rock paintings occur' (Malan and Cooke, 1941: 300). Subsequently, Wonderwerk has become increasingly recognized for its long sequence of artefacts, fossils and environmental information (Avery, 1981, 1995; Beaumont, 1979, 1982, 1990, 2004; Camp, 1948; Humphreys and Thackeray, 1983; Malan and Wells, 1943; Thackeray, 1984; Van Zinderen Bakker, 1982). Particularly important is the sequence of Middle Pleistocene fossils, which is unique in South Africa. Early reports concentrated on the larger mammal remains from Wonderwerk but extensive excavations by P.B. Beaumont, McGregor Museum, Kimberley, yielded impressively large samples of micromammals from several excavations in this huge (149 m deep; Beaumont (2004)) cave (Fig. 1). The Holocene (Later Stone Age) sample showed high taxonomic diversity, with 3731 individuals representing at least 33 species in 30 genera (Avery, 1981) while material from a test excavation into the Pleistocene layers produced 2966 individuals representative of at least 27 species in 23 genera (Avery, 1995). Currently, M. Chazan (University of Toronto) and L. Kolska Horwitz (University of Jerusalem) are leading an international team to carry forward Beaumont's work, with particular emphasis on dating the deposits and confirming correlations of excavations in different areas of the site. The present investigation, although begun before the current initiative, forms part of the Chazan–Horwitz project.

The sheer size of the micromammalian samples available from Wonderwerk Cave has brought with it unanticipated logistical problems, which have been exacerbated by a high degree of breakage. The fundamental reason for the high level of breakage is the fragile condition of much of the bone. However, the situation has almost certainly been made worse by the long drawn-out process involving excavation, transport to Kimberley and initial sorting there under Peter Beaumont's supervision, followed by transport to Cape Town and detailed sorting at Iziko South African Museum under my supervision.

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On the positive side, however, the extent of the excavations and the correspondingly large amounts of micromammalian material highlight problems that might otherwise have remained hidden and undetectable. For this reason, examining the potential pitfalls that are exposed at Wonderwerk has the dual benefit of allowing one both to assess the level of accurate interpretation possible for this site and to highlight potential areas of concern at other sites where they may be less obvious. Specifically, identification and counting, and their effects on sample content and structure are considered. Some suggestions are also made for future taphonomic work.

2. The site and excavation

Wonderwerk Cave is a dolomite cavern, which dips 1° into the mountainside (Butzer, 1984a) and whose geology was first outlined by Malan and Cooke (1941) and Beaumont (1979). Butzer (1984a, b) subsequently conducted detailed analyses of the sedimentology and geochemistry based on two composite sequences, one from excavated sections 18–32 m from the cave mouth and the other from existing outcrops at 41–62 m. The front profile, identified as WB, covers a depth of 4.22 m while the interior profile (WA) reaches a depth of 2.10 m (Butzer, 1984a). Although many of the deposits are more or less horizontal, there is also variable dipping in parts of the cave. The dip is characterized generally as being up to 5° towards the interior (approximately southwards) in deposits forward of the stalagmite but only 1–2° behind the stalagmite (Butzer, 1984b), but Butzer (1984a) records a 10° westerly dip in the lower part of the WB section. According to Butzer (1984a) the primary grit and sand fraction must have been introduced into the cave by water action, especially along the eastern side of the drip line, since wind velocity would have been insufficient to transport such material. Moreover, large-scale erosion in the cave is attributed to repeated surges of run-off down the cliff face and into a former sluice on the western side of the cave (Butzer, 1984a). This interpretation is, however, disputed by Beaumont (pers. comm. 2006.), who notes that the deposits provide no evidence of the posited channels and that no water movement inwards can be seen nowadays during heavy downpours.

Beginning in 1978, Beaumont conducted excavations into the Pleistocene deposits in eight different areas of the cave (Beaumont, 1990), material from four of which is discussed in this paper (Fig. 1). These deposits contain predominantly Earlier Stone Age cultural material of an apparent Middle Pleistocene age but precise dating and archaeological analyses have yet to be completed. Deposits from the various excavations were grouped into 10 site-wide Major Units (MUs), each about 0.5 m thick (Beaumont, 2004) (MU1, the uppermost unit, is Holocene and not included in this analysis). Each MU comprises one or more numbered strata in one or more excavations (Table 1). In both MUs and strata the numbering begins at the top of the sequence. MU 2 is represented by material from Excavation 5 stratum 2, other samples being disregarded at this stage because they have not been confirmed as in situ (P.B. Beaumont, pers. comm. 2006). MU 3 is represented by samples from Excavations 2 and 6, and MU 4 by samples from Excavations 1 and 6 (Table 1). Deposits from MU 5 downwards are only represented in Excavation 1.

Table 1
Numbered strata yielding micromammalian samples discussed, with their allocation to Major Units (MUs) by P.B. Beaumont (pers. comm. 2004)

Major Unit	Exc.1	Exc. 2	Exc. 5	Exc. 6
MU2			2	
MU3		3		3LR, 4
MU4	6			5
MU5	7			
MU6	8			
MU7	9			
MU8	10			
MU9	11			
MU10	12			

See text for further details.

Where possible, Beaumont excavated natural strata whose upper and lower surfaces were excavation-wide in extent. Substrata, usually of more limited distribution, occurred in some of them. When internal stratigraphy was absent, removal was by (mainly 5 cm) spits parallel to the stratum surface (P.B. Beaumont, pers comm. 2006). Each excavation covered a varying number of square feet (Beaumont used the original grid laid out by Malan and Cooke (1941)) with a combined depth of about 7 m (Beaumont, 2004). The distribution of the squares yielding micromammalian samples is shown in Fig. 1. Excavations 1 and 6, which are located at the front and back of the cave, respectively (Figs. 1 and 2), produced extremely large quantities of micromammalian remains (Table 2). Although concentrations are reduced below MU 10, there are micromammalian remains throughout the sequence, the lowest specimen in the available collections being a macroscelidid elephant shrew anterior mandible from spit 85–90 in square T33 of MU 12.

3. Collection and preparation

The unconsolidated sediment was dry-screened through a 1 mm screen, with or without a 0.5 mm screen on top. The 0.5 mm screen was only used when the deposit was mainly fine sand; for the coarser material the 1 mm screen was used alone because this permitted some of the grit to filter through, thus reducing damage to the more fragile bone fragments (P.B. Beaumont, pers. comm. 2006). During initial sorting in Kimberley all micromammalian material was extracted from the bulk samples. Maxillae and mandibles, whole and partial, were subsequently extracted from the initial sort in preparation for ecological and environmental analysis. The remaining elements, including loose teeth, were retained pending use in a full taphonomic analysis.

For ease of reference strata have been assigned codes comprising three digits with an appended letter where required. The first digit refers to the excavation (see Fig. 1) and the following two digits refer to the stratum within that excavation (Table 1). Thus, for example, the second

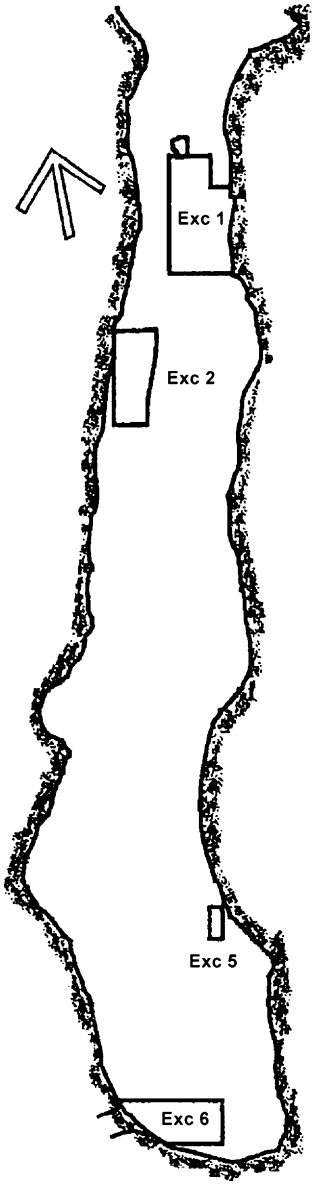

Fig. 1. Ground plan of Wonderwerk Cave (after Beaumont, 2004) showing location and extent of excavations discussed in this paper. The cave is approximately 150 m deep.

stratum in Excavation 5 is designated 5.02. To identify 5 cm units within a stratum two further digits were added: for example, 5.02.00 refers to spit 00–05 cm in stratum 02 of Excavation 5. In total, 1888 samples of micromammalian mandibles and maxillae were extracted from initial samples. Being relatively small and few in number, all samples from strata 2.03 and 5.02 were examined. In Excavations 1 and 6 there were a great many samples, some very large but many small. To expedite matters it was decided to give priority to the larger samples in these excavations and to leave the small samples for possible later examination. This course of action produced 281 samples for examination; of these, 17 contain over 1000 individuals, a further 157 comprise between 50 and 999 individuals, and the remaining 107 contain fewer than 50 individuals. The fact that not all the samples from each stratum have been examined could introduce biases that would prohibit meaningful comparison between strata. To circumvent this potential problem it was decided to standardize comparisons on 5 cm samples containing 50 and more individuals. These samples were derived, on occasion, from more than one square foot. The resulting database comprised 95 samples, hereafter called spit-samples to distinguish them from the total complement of samples.

4. Identification and sample content

The need for a key to small mammals based solely on cranial characters was recognized by Hanney (1962), who published such a key for Malawi. The idea was subsequently developed by Coetzee (1972), who published a southern African key expressly for the identification of remains from owl pellets. Such keys can be extremely useful when one is dealing with complete or nearly complete skulls. Since, however, this is seldom the case, even in the best preserved archaeological or palaeontological samples, tooth cusp patterns have assumed pre-eminence as a means of identifying specimens. The situation is further complicated when, as at Wonderwerk, most specimens are represented by fragmentary jaws (both maxillae and mandibles) from which the teeth have been lost (this is not to say that loose teeth do not occur at Wonderwerk but, as was noted above, only jaws have so far been counted). Non-dental elements therefore became the principal identifying elements. In particular, alveolar patterns have been relied upon heavily. The usefulness of studying alveolar patterns, which is a logical extension of the established practice of counting tooth roots, was first pointed out by Davis (1965) (Appendix 1). Davis's (1965) illustrations of the alveoli of selected murine species are augmented here in Figs 2 and 3 to include representatives of all Muridae genera identified from Wonderwerk. Other features, such as the location of mental and palatal foramina, muscle attachments and origination of the zygomatic, have also proved useful. Appendices 2 and 3 provide keys based on these characters. These keys may be considered as pragmatic rather than formal because the conventional elimination format has been augmented by supplementary information that may be used to cross-check identifications. Indications of size have been given where the terms 'large', 'small', etc. are used but it is not considered useful to provide more detailed measurements because of the potential for geographic and temporal variation. This has yet to be investigated and will probably prove more pertinent to identification at the species level. However, Roberts (1951) provides a great deal of mensural data for modern taxa. Finally, although the keys are restricted to taxa represented at Wonderwerk, they can be modified and expanded to include other taxa using the same or similar features. They can therefore be seen as templates as much as definitive keys.

The combination of badly broken material and large numbers meant that it was not practicable at this stage to take identifications below the level of genus. However, it is readily

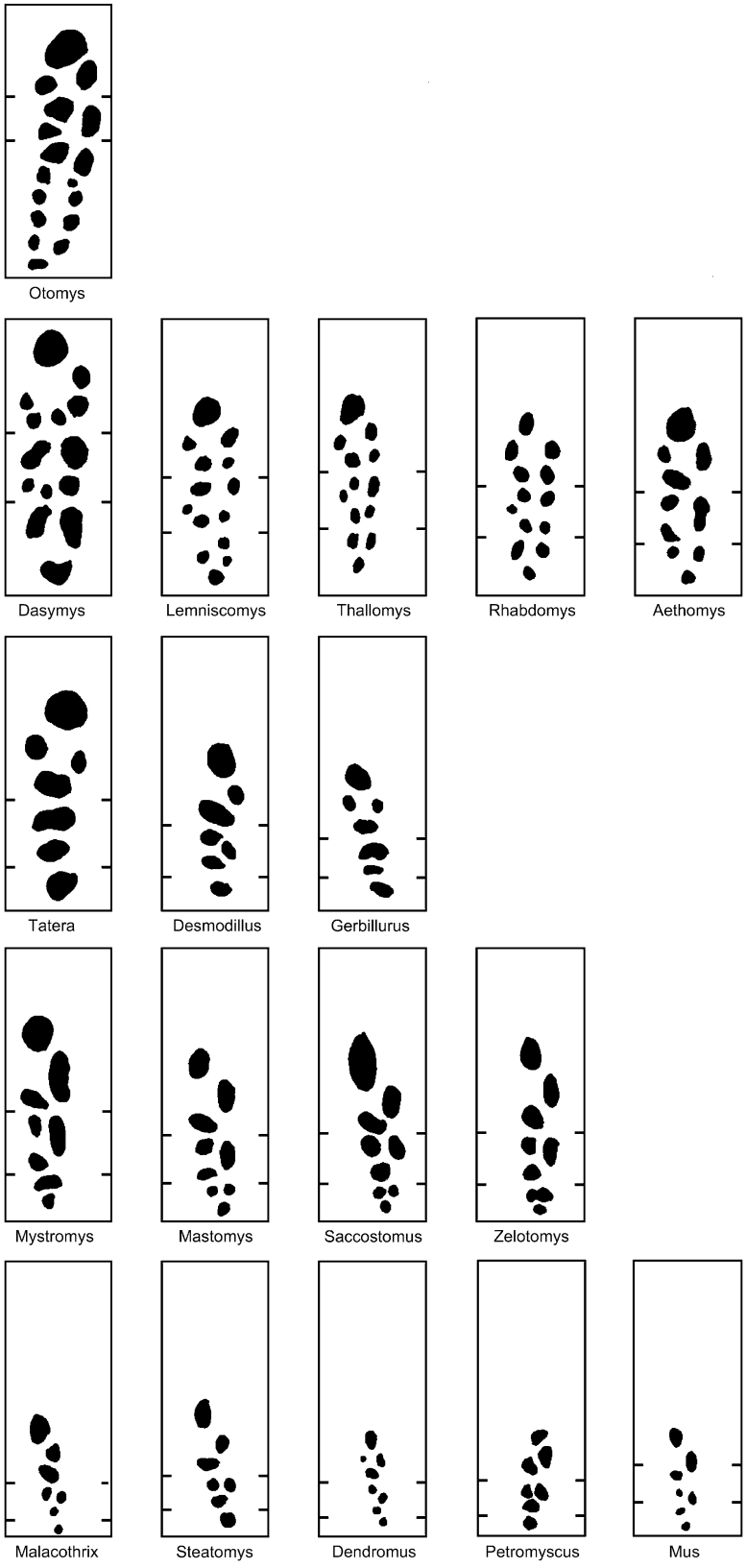

Fig. 2. Alveolar patterns of selected murid right maxillae. Horizontal marks indicate breaks between alveoli of individual teeth, with M^1 at the top. 400× actual size. See Appendix 2 for further information.

Table 2
Numbers of samples examined from each stratum or sub-stratum, together with the total minimum number of individuals (MNI) so far recorded for each, and the maximum MNI in any one spit-sample in that stratum or sub-stratum

Stratum	No. of samples	Total MNI	Max. MNI per spit-sample
5.02	36	1581	402
2.03	29	734	594
6.03	18	9102	1487
6.04	9	9447	1265
6.04a	3	1375	624
6.04b	10	13,069	5355
6.05	24	894	218
1.06	37	2345	535
1.07	28	3576	756
1.07b	2	287	187
1.07br	4	280	150
1.08	2	682	407
1.08a	1	65	65
1.09b	7	677	454
1.09c	6	1242	419
1.09d	3	661	304
1.09e	8	5868	2114
1.10	35	12,131	2250
1.11	1	365	365
1.12	17	780	379
1.12a	1	5	5
Total	281	65,166	

apparent that seven of the 34 or 35 genera represented include material from more than one species (Table 3). By far the best represented of the five orders present is the Rodentia (Table 4). At this level only the Order Eulipotyphla (represented by the Soricidae, shrews) is better represented than the Rodentia in any spit-sample. Within the Rodentia only the Family Muridae dominates any spit-sample (Table 4). Although eight of the 20 murid genera belong in the Murinae, in terms of numbers of individuals this is the dominant murid sub-family in only 3.2% of cases; Gerbillinae, with approximately a third of total murid individuals, is the dominant murid sub-family in 64.2% of the spit-samples.

All taxa can potentially be reliably identified, albeit with increasing difficulty as one approaches the species level where the differences are slighter; it is merely a question of determining which features reliably distinguish the taxa at a given level, as was discussed above. However, it is likely that the finer the distinction the more specimens it will require to confirm the constancy of the feature employed, although this has yet to be tested because identification to the species level has not been undertaken. Initial examinations have revealed that at least seven genera comprise more than one species but their identities have yet to be confirmed. At this taxonomic level it is much more difficult to ensure accurate and consistent identification and further detailed examinations are required to establish the extent to which this is possible in current sample. In general, however, one can conclude that there need be no bias in the identification of taxa within a sample, provided one spends sufficient time determining the relevant features and confirming accuracy and consistency of identification.

5. Minimum numbers of individuals and sample structure

The highest number of any one jaw (left and right mandibles and maxillae) was generally taken as providing the minimum number of individuals (MNI) in each genus. The sole exception was the Soricidae (shrews) where only mandibles were counted because there were too few maxillae preserved to warrant including them. To standardize counting, jaws were only counted if they included a certain element, which was chosen for the pragmatic reason that it is commonly preserved, as discussed below. The Chiroptera (bats) were the exception in that any portion of a jaw was counted because there was generally only one individual represented. The same could, of course, be said of certain other ill-represented taxa such as the Eulipotyphla (Chrysochloridae, golden moles) but it was decided to restrict exceptions to the one order that is not generally employed in interpretations. The scores for each jaw were entered into a Microsoft Excel worksheet, in which minimum numbers of individuals and scores for various units in the excavation were calculated.

In view of the scale of the project and the amount of time involved in achieving these counts it was decided to examine the possibility of streamlining the process by identifying and counting only upper or lower jaws. In theory this should halve the time needed. Because soricid maxillae had already been excluded, the only alternative to counting all jaws would be to restrict attention to mandibles. The ratio of MD/MNI, where MD is obtained from mandibles only, shows great variation; the mean ratio for 35 genera in 95×5 cm spits was 0.84, with a range of 1.00–0.25 (Table 5). More serious for interpretational purposes is the variation among taxa. Superficial examination of the raw scores showed that gerbil maxillae outnumbered mandibles in most samples examined. This impression was confirmed by the MD/MNI ratio, which is 0.59 for the Gerbillinae as a whole, 0.62 in *Gerbillurus* and 0.56 in *Tatera* (Table 5). At the other end of the spectrum, the ratio is 0.97 for the Macroscelididae (*Elephantulus*/*Macroscelides*), 0.96 for *Mastomys* and 0.95 for *Dendromus.* This indicates that proportional representation of different taxa within a sample will be demonstrably skewed if only mandibles are counted. The only possibility for rectifying this situation would be to vary the jaw counted depending on which is normally best represented in taxa. Even if such manipulation were justified it would still be necessary to confirm the correct jaw to count in each sample because the same jaw does not consistently outnumber the other; in some cases, such as the Otomyinae, although mandibles have normally been found to outnumber maxillae (pers. obs.) in the present case they do not. The time-saving justification would therefore be invalidated, leading to the conclusion that for groups other than Soricidae both maxillae and mandibles should be counted to find the best approximation of the original MNI.

Given the necessarily pragmatic nature of the identification exercise (Appendices 1 and 2), features used for counting vary to some extent from one order to another. The

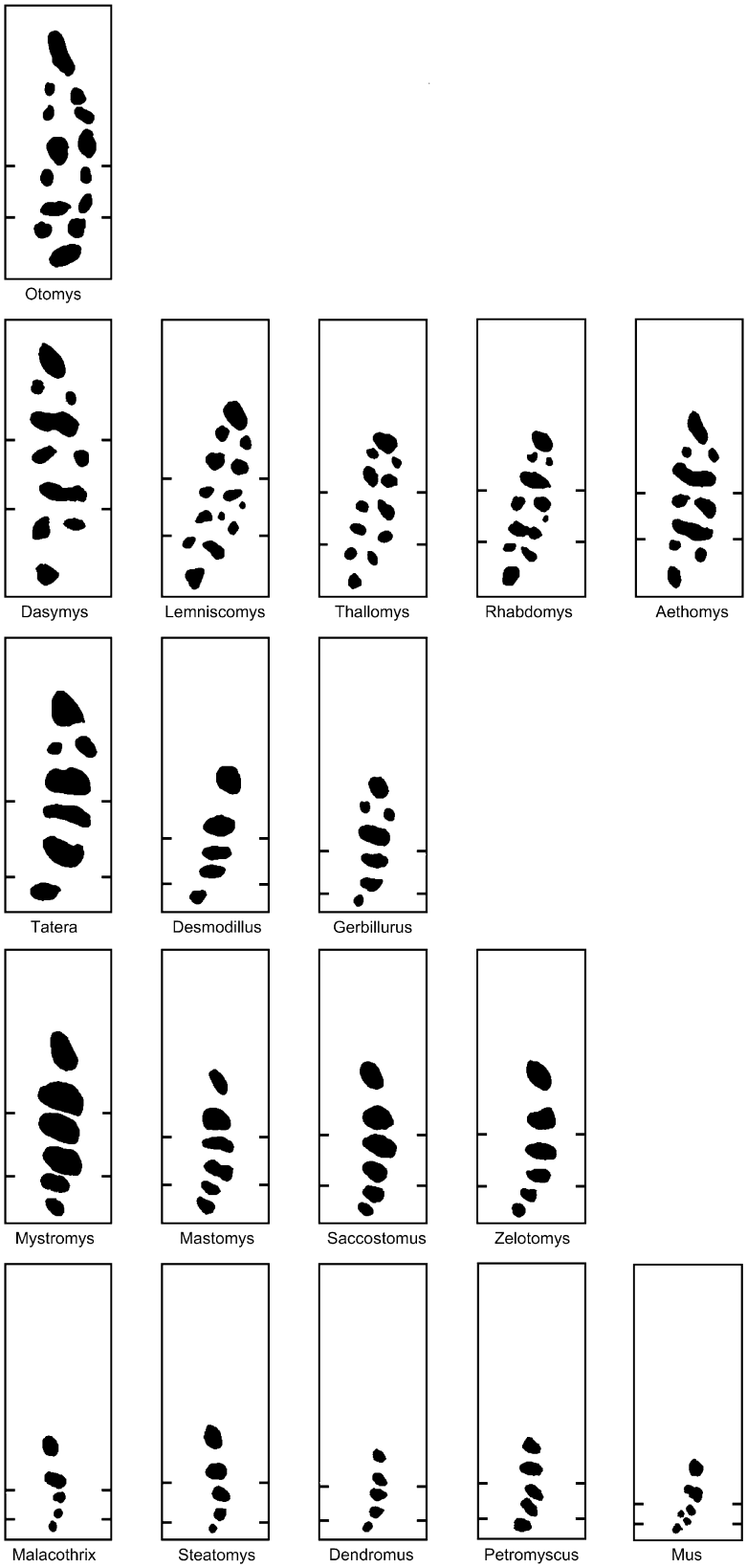

Fig. 3. Alveolar patterns of selected murid right mandibles. Horizontal marks indicate breaks between alveoli of individual teeth, with M_1 at the top. 400× actual size. See Appendix 3 for further information.

Table 3
Genera represented in Pleistocene deposits at Wonderwerk Cave, with the number of spit-samples in which they occur (No.) and the highest percentage representation (%) in any one of the 95 spit-samples

Order	Family: Sub-family	Genus (No. spp.)	Common name	No.	%
Afrosoricida	Chrysochloridae	*Chrysospalax*	Golden mole	3	0.2
		Chlorotalpa	Golden mole	27	1.5
Macroscelidea	Macroscelididae	*Macroscelides et/aut Elephantulus*	Elephant shrew	95	22.8
Rodentia	Bathyergidae	*Cryptomys*	Molerat	88	8.8
	Myoxidae	*Graphiurus*	Dormouse	14	0.8
	Muridae: Murinae	*Lemniscomys*	Grass mouse	28	3.0
		Rhabdomys	Grass mouse	82	2.5
		Zelotomys	Desert mouse	75	6.9
		Dasymys	Marsh rat	8	0.6
		Mus	Pygmy mouse	73	3.9
		Mastomys	Multimamate mouse	87	9.2
		Thallomys	Tree rat	13	0.8
		Aethomys (2)	Rock mouse	94	16.0
	Muridae: Otomyinae	*Otomys* (3)	Vlei rat	95	31.3
	Muridae: Gerbillinae	*Desmodillus*	Short-tailed gerbil	68	4.1
		Gerbillurus (2)	Hairy-footed gerbil	95	18.9
		Tatera (2)	Gerbil	95	36.9
	Muridae: Mystromyinae	*Mystromys*	White-tailed mouse	95	15.9
	Muridae: Cricetomyinae	*Saccostomus*	Pouched mouse	86	12.8
	Muridae: Dendromurinae	*Malacothrix*	Gerbil mouse	90	3.7
		Dendromus (2)	Climbing mouse	92	16.8
		Steatomys	Fat mouse	90	18.1
	Muridae: Petromyscinae	*Petromyscus*	Rock mouse	61	4.0
Eulipotyphla	Soricidae	*Myosorex*	Forest shrew	82	10.9
		Suncus (*Crocidura*)	Dwarf shrew	69	9.3
		Crocidura (3 or 4)	Musk shrew	92	29.5
		Crocidura et/aut Myosorex		95	36.6
Chiroptera	Molossidae	*Sauromys*	Free-tailed bat	1	0.1
		Tadarida	Free-tailed bat	16	0.8
	Vespertilionidae	*Miniopterus*	Long-fingered bat	22	1.3
		Neoromicia	Pipistrelle	8	0.4
		Cistugo[a]	Hairy bat	0	0
		Eptesicus	Serotine bat	2	0.2
	Nycteridae	*Nycteris*	Slit-faced bat	2	0.4
	Rhinolophidae	*Rhinolophus* (3 or 4)	Horseshoe bat	61	2.0

The probable number of species is given in brackets where more than one per genus. Taxonomic list after Bronner et al. (2003).
[a] Only represented by one specimen, not from a spit-sample.

choice of feature depends on which has been observed to be most frequently preserved. This, in turn, naturally depends on the strength of the various structures, which varies from one order to another. Thus, it has been found that in rodents the anterior portion, with all or part of the first molar or its alveoli, is generally well preserved in both upper and lower jaws. The one rodent exception is the mandible in Bathyergidae, where the posterior portion is the most frequently preserved, as it is in both soricid shrews and macroscelidid elephant shrews. For maxillae of the latter the posterior part in the region of the zygomatic attachment was counted. This sturdy element, which is frequently preserved, also has the potential for allowing distinction of *Macroscelides* from *Elephantulus* but this requires further investigation. On occasion the anterior portion of elephant shrew mandibles would have provided a higher count than the posterior portion but this did not occur sufficiently often to warrant changing the counted feature.

The effect of differential difficulty of identification on establishing minimum numbers of individuals has also to be considered. Whereas it is a relatively simple matter, with attention to detail, to identify the taxa represented in a sample, arriving at a count of individuals is affected by various considerations. One of these concerns the fact that jaws appear to have an equal chance of being correctly identified to the family level but not below that. This is because, while difficulty of identification increases over all with decreasing taxonomic level, the degree of difficulty is not closely correlated with taxonomic level. For instance, within the Muridae, the very distinctive multiple-alveolar pattern of the otomyines (Figs. 2 and 3) means that even a small part of any jaw can be identified to sub-family and, indeed, genus. The anterior portions of mystromyine (*Mystromys*) and gerbilline jaws are reasonably distinctive, although the difference between *Gerbillurus* and *Desmodillus* is not always clear. Jaws of the other murid sub-families are much

Table 4
Minimum number of individuals (MNI) in 95 spit-samples (N = total sample size at the various taxonomic levels), maximum percentage representation (Maximum) at various taxonomic levels in any one of the spit-samples, and percentage of spit-samples in which each taxon is dominant (Dominance)

		MNI	Maximum	Dominance
Orders ($N = 55{,}777$)	Afrosoricida	43	1.5	0.0
	Macroscelidea	3598	22.8	0.0
	Rodentia	35,682	88.5	87.5
	Eulipotyphla	16,243	59.2	12.5
	Chiroptera	211	2.6	0.0
Rodentia ($N = 35{,}682$)	Bathyergidae	1286	10.8	0.0
	Myoxidae	15	1.4	0.0
	Muridae	34,381	100.0	100.0
Muridae ($N = 34{,}381$)	Murinae	6523	28.6	3.2
	Otomyinae	5005	47.3	16.8
	Gerbillinae	11,772	55.6	64.2
	Mystromyinae	4333	23.9	0.0
	Cricetinae	1019	19.7	0.0
	Dendromurinae	5457	56.1	15.8
	Petromyscinae	272	5.9	0.0
Genera ($N = 55{,}777$)	*Elephantulus*/*Macroscelides*	3598	22.8	8.3
	Otomys	5005	31.3	17.7
	Gerbillurus	5841	18.9	1.0
	Tatera	5601	36.9	30.2
	Mystromys	4333	15.9	1.0
	Crocidura	5885	29.5	2.1
	Myosorex/*Crocidura*	8415	36.6	39.6

All represented taxa shown, except in the case of genera, where only those dominant in at least one spit-sample are listed. See text for further details and Table 3 further information on genera.

more difficult to distinguish unless a greater portion of the jaw is preserved. In the latter case, it is sometimes easier to distinguish genera within one sub-family than it is across sub-families (see Appendices 2 and 3); the Murinae include genera with Davis's (1965) simple and complex alveolar patterns whereas simple patterns occur in three different sub-families (Figs. 2 and 3).

Differential difficulty of identification cannot simply be solved by spending more time on some specimens than others. It also requires more detailed (or greater numbers of) features to allow identification to be effected. Whether these features are found depends, in turn, on patterns and degrees of breakage. Again using the murid sub-families as an example, it will matter very little how the otomyine jaws are broken, as long as they have the counted section, because they are so distinctive. In the gerbillines and *Mystromys* it is fortunate that it is the counted, anterior portions of the jaws that are distinctive and allow easy generic identification. More specifically, in *Mystromys* mandibles the anterior and posterior alveoli of M_1 are widely spaced (Fig. 3) with the bone between apparently strengthening the jaw, which is frequently broken immediately posterior to this point, so that even this small section of the mandible is distinctive enough to allow identification. In many other taxa this small section could be insufficient to distinguish one of several possibilities with the result that the jaw portions would have to be set aside as unidentified. As a result the possibility arises that *Mystromys* mandibles, in this example, could be over-counted relative to less distinctive mandibles of similar species. In the case of the soricid shrews, which are much more vulnerable to breakage, many mandibles are broken in such a way as to remove diagnostic features. In consequence there is a very high number of imprecisely identified soricid shrews (Table 3). Only controlled experiments will allow determination of the truth or otherwise of the assertion that distinctiveness, possibly combined with susceptibility to breakage, is likely to have differential effects on identification and therefore on counts.

6. Future taphonomic work

A full taphonomic examination is beyond the scope of the present paper but, in the meantime, a few comments may be appropriate to clarify certain issues discussed here and to point the way for future work. While taphonomy should cover all aspects of a fossil's journey from death of the original animal to description and interpretation of the fossil in the laboratory, parts of the process are often either ignored or underplayed. Undoubtedly, aspects of the taphonomic history will have a greater or lesser effect on the end sample from different sites and it can be argued that identifying these aspects should form an explicit part of any full taphonomic analysis. In the present case, interpretation is apparently heavily affected by the amount and type of breakage that occurred during and after excavation. Undertaking a customized control excavation would allow this supposition to be tested. Thereafter, the effect of other factors, such as the nature of the deposits and the identity of the accumulator, could be considered. In the latter case, examination of body-part representation will require consideration of the effects of screening through differently sized sieves. It is quite likely that even the 0.5 mm screen will not have retained all the teeth of the many small taxa represented so it will not be possible with the present samples to determine accurately the relative loss of teeth. This contention also needs testing by a comparative excavation. Casual inspection did not suggest any rolling that might have indicated water action or other movement but detailed surface examination has yet to be conducted. Resolution of the issue of site formation, based on other lines of evidence, will also have a bearing on interpretation of the lateral distribution of micromammalian remains within the site as a whole. In sum, Wonderwerk has the potential to shed light on various issues concerning micromammalian taphonomy but this potential can only be fulfilled through acquisition of a sample that conforms to current standards for taphonomic data collection.

7. Conclusions

The very large but badly damaged micromammalian sample from Wonderwerk Cave allows various issues to be examined and suggestions to be made for further consideration.

- Large samples can allow long-assumed truths to be quantified and thus confirmed or rejected.

Table 5
Ratio (MD/MNI) of counts of individuals in supra-generic taxa (Orders, Families and murid Sub-Families) and selected genera

Order	Family	Sub-family	Genus	Samples	Mean ratio	Minimum ratio	% Equal scores
Orders							
Afrosoricida	(Chrysochloridae)			28	0.91	0.00	89.3
Macroscelidea	(Macroscelididae)		(*Macroscelides*/*Elephantulus*)	95	0.97	0.50	86.3
Rodentia				95	0.75	0.37	0.0
Eulipotyphla	(Soricidae)			95	1.00	1.00	100.0
Chiroptera				70	0.93	0.00	88.6
Families							
Rodentia	Bathyergidae		(*Cryptomys*)	88	0.89	0.00	80.7
	Myoxidae		(*Graphiurus*)	14	0.93	0.00	92.9
	Muridae			95	0.75	0.36	0.0
Eulipotyphla	Soricidae			95	1.00	1.00	100.0
Chiroptera	Molossidae			16	0.94	0.00	93.8
	Vespertilionidae			28	1.00	1.00	100.0
	Nycteridae		(*Nycteris*)	2	1.00	1.00	100.0
	Rhinolophidae		(*Rhinolophus*)	61	0.92	0.00	88.5
Murid sub-families							
Rodentia	Muridae	Murinae		95	0.81	0.22	16.8
		Otomyinae	(*Otomys*)	95	0.70	0.13	13.7
		Gerbillinae		95	0.59	0.25	3.2
		Mystromyinae	(*Mystromys*)	95	0.91	0.14	53.7
		Cricetomyinae	(*Saccostomus*)	86	0.87	0.25	55.8
		Dendromurinae		95	0.87	0.00	23.2
		Petromyscinae	(*Petromyscus*)	61	0.88	0.00	80.3
Genera							
Rodentia	Muridae	Murinae	*Rhabdomys*	82	0.74	0.00	54.9
			Mastomys	87	0.96	0.00	88.5
			Aethomys	94	0.73	0.19	25.5
		Gerbillinae	*Gerbillurus*	95	0.62	0.00	10.5
			Tatera	95	0.56	0.00	5.3
		Dendromurinae	*Malacothrix*	90	0.58	0.00	31.1
			Dendromus	92	0.95	0.40	80.4
			Steatomys	90	0.91	0.33	64.4
Eulipotyphla	Soricidae		*Myosorex*	82	1.00	1.00	100.0
			Crocidura	92	1.00	1.00	100.0
			Myosorex/*Crocidura*	95	1.00	1.00	100.0

MD, counts based on mandibles only; MNI, counts based on both maxillae and mandibles; samples, number of spit-samples in which the taxon occurs; % Equal scores, is the percentage of samples in which MD provided the same number of individuals as MNI. The maximum ratio is 1.00 in all cases except Rodentia and Muridae, where it is 0.98. Taxa in brackets are sole representatives of the next highest taxon, e.g. (Chrysochloridae) is the only Family representing the Order Afrosoricida at Wonderwerk. The scores are therefore the same for the highest taxon as for the lowest taxon indicated.

- Alveolar patterns and other non-dental features such as the location of mental and palatal foramina, muscle attachments and origination of the zygomatic provide reliable identifications even in the absence of teeth.
- The keys provided can be used either to identify the particular taxa or as a basis for developing keys for other taxa.
- Micromammalian jaws have an equal chance of being identified down to the family level but below that degrees of difficulty in identification vary among taxa.
- Large samples are important to confirm consistency of identification features.
- Minimum numbers are more reliably achieved when based on both maxillae and mandibles than when based solely on mandibles because some taxa are preferentially represented by maxillae and some by mandibles.
- Differential difficulty in identification, especially combined with relative susceptibility to breakage, has the potential to influence counts in badly broken samples.
- A customized taphonomic excavation is required as part of a full taphonomic analysis, to establish the relative impact of original collection methods.

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Appendix 1

Muridae: number of alveoli with number of rootlets in Roman numerals in brackets. Data for maxillae before the colon, for mandibles after the colon. Based on Davis (1965).

Sub-family	Genus	Alveolar formula
Cricetomyinae	*Saccostomus*	3(i)–3–3:2–2–2
Dendromurinae	*Dendromus*	3(i)–3–1:2–2–1
	Steatomys	3–3–1:2–2–1
	Malacothrix	3–3–1:2–2–1
Gerbillinae	*Tatera*	4–2–1:2(ii)–2–2
	Desmodillus	3–2–1:2(i)–2–2
	Gerbillurus	4–2–1:2(ii)–2–2
Murinae	*Aethomys*	4–3–3:2(i or ii)–3–2
	Dasymys	4(i)–4–3(i):2(ii)–3–3
	Lemniscomys	5–4(iii)–3:2(ii)–4(ii)–3
	Mastomys	3–3–2:2–2–2
	Mus	3–3–1:2–3–1
	Rhabdomys	5–5–3:2(ii)–3(i)–2
	Zelotomys	3–3–2:2–2–2
	Thallomys	5–4–3:2(ii)–2–3
Mystromyinae	*Mystromys*	3–3–2:2–2–2

Appendix 2

Features used to distinguish maxillae of Wonderwerk micromammals in the absence of diagnostic teeth. Numbers of teeth or alveoli refer to half maxilla. See Roberts (1951) for further measurements, and text for further discussion.

Orders		
1	Diastema between incisors and cheekteeth	Rodentia
	No diastema between incisors and cheekteeth	2
2	No zygomatic arch	Eulipotyphla: Soricidae
	Zygomatic arch present	3
3	Greatest maxillary width & zygomatic origination anterior to last cheek tooth; prominent premaxillae extending anterior to palate	Afrosoricida: Chrysochloridae
	Greatest maxillary width & zygomatic origination at last cheek tooth; premaxillae not prominent	4
4	Large incisive & palatal foramina	Macroscelidea: Macroscelididae
	Small incisive & palatal foramina	Chiroptera

Rodentia families		
1	Alveoli for three cheekteeth, one incisor	Muridae
	Alveoli for four cheekteeth, one incisor	2
2	Palate narrow, much less than length of cheekteeth alveoli; anterior cheek tooth largest	Bathyergidae: *Cryptomys*
	Palate broad, approximately equal to length of cheekteeth alveoli; anterior cheek tooth smallest	Myoxidae: *Graphiurus*

Appendix 2 (*continued*)

Muridae sub-families and genera		
1	Multiple alveoli; M^3 longest cheek tooth; palate very narrow with broad region of contact between two halves	Otomyinae: *Otomys*
	Five or fewer alveoli; M^1 longest cheek tooth; palate broader	2
2	M^1 with five alveoli	3
	M^1 with four alveoli	8
	M^1 with three alveoli	10
3	Large (anterior–posterior length of M^1 alveoli above 3 mm)	Murinae: *Dasymys*
	Smaller (anterior–posterior length of M^1 alveoli 3 mm and less)	6
6	Anterior palatal foramina do not penetrate beyond level of anterior alveoli of M^1	Murinae: *Lemniscomys*
	Anterior palatal foramina penetrate to level of anterior labial alveolus of M^1	7
7	Slightly larger (anterior–posterior length of M^1 alveoli $\pm$ 2.4 mm); prominent anterior alveolus; remaining alveoli set in square	Murinae: *Thallomys*
	Slightly smaller (anterior–posterior length of M^1 alveoli $\pm$ 2.2 mm); anterior alveolus moderately prominent; central pair of alveoli farther apart than posterior pair	Murinae: *Rhabdomys*
8	M^1 with large round anterior and posterior alveoli separated by two smaller round alveoli	9
	M^1 with relatively large anterior alveolus, oval or elongate lingual alveolus & smaller labial & posterior alveoli	Murinae: *Aethomys*
9	Large (anterior–posterior length of M^1 alveoli $\pm$ 3.6 mm in *T. leucogaster*)	Gerbillinae: *Tatera*
	Small-medium (anterior–posterior length of M^1 alveoli $\pm$ 2.6 mm); medial labial alveolus reduced or missing	Gerbillinae: *Desmodillus*
	Small (anterior–posterior length of M^1 alveoli $\pm$ 2.3 mm in *G. paeba*)	Gerbillinae: *Gerbillurus*
10	Long anterior palatal foramina reaching between elongated or oval lingual roots of M^1	11
	Shorter anterior palatal foramina not reaching between round lingual roots of M^1	12
11	Larger (anterior–posterior length of M^1 alveoli $\pm$ 3.6 mm); M^1 with prominent long lingual alveolus	Mystromyinae: *Mystromys*
	Smaller (anterior–posterior length of M^1 alveoli $\pm$ 2.7 mm); M^1 with oval less prominent lingual alveolus	Murinae: *Mastomys*
12	Larger (anterior–posterior length of M^1 alveoli $\pm$ 3.1 mm)	13
	Small (anterior–posterior length of M^1 alveoli $<$ 2.4 mm)	14
13	M^1 with anterior alveolus separated from lingual and posterior alveoli	Cricetomyinae: *Saccostomus*
	M^1 with alveoli closer together	Murinae: *Zelotomys*
14	Masseter knob present	15
	No masseter knob	17
15	Elongated M^1; lingual alveolus nearly in line with anterior and posterior alveoli; masseter knob ridge-shaped	Dendromurinae: *Malacothrix*

Appendix 2 (*continued*)

Muridae sub-families and genera		
	M^1 not elongated; lingual alveolus not in line with anterior and posterior alveoli; masseter knob not ridge-shaped	16
16	Larger (anterior–posterior length of M^1 alveoli ± 2.2 mm)	Dendromurinae: *Steatomys*
	Smaller (anterior–posterior length of M^1 alveoli < 2.0 mm)	Dendromurinae: *Dendromus*
17	Anterior palatal foramina do not penetrate beyond level of anterior alveoli of M^1; alveoli of M^1 equally spaced; single alveolus for M^3	Petromyscinae: *Petromyscus*
	Anterior palatal foramina penetrate to level of labial alveoli of M^1; anterior alveolus of M^1 widely separated from labial and posterior alveoli; two alveoli for M^3	Murinae: *Mus*

Eulipotyphla (Soricidae)		
1	Three single-rooted unicuspid teeth	*Crocidura*
	Four single-rooted unicuspid teeth	2
2	Larger (anterior–posterior length of unicuspid alveoli ± 2.6 mm in *M. varius*); posterior single-rooted unicuspid tooth much reduced	*Myosorex*
	Smaller (anterior–posterior length of unicuspid alveoli ≤ 2.0 mm); posterior single-rooted unicuspid tooth moderately reduced	*Suncus*

Afrosoricida (Chrysochloridae)	
Large (total alveolar length ± 16.7 mm in *C. trevelyani*); maxilla relatively long	*Chrysospalax*
Small (total alveolar length ± 9.5 mm); maxilla broader, nearly triangular	*Chlorotalpa*

Macroscelidea (Macroscelididae)	
Smaller (anterior–posterior length molar alveolar row < 6.0 mm); maxilla relatively short and broad; alveoli of anterior unicuspids close together; pronounced knob at relatively acute angle between zygomatic and maxilla	*Macroscelides*
Larger (anterior–posterior length molar alveolar row > 6.0 mm); maxilla relatively longer; alveoli of anterior unicuspids more widely spaced; no pronounced knob at more obtuse angle or arch between zygomatic and maxilla	*Elephantulus*

Chiroptera families (after Roberts, 1951)	
Frontal region narrowly constricted; nasal bulbs higher than frontals	Rhinolophidae
Frontal region broad & hollowed by raised, thin, laterally expanded plates	Nycteridae
Premaxillae more or less divided distally by a space between lateral sections, which are crushed against the maxilla and bear incisors; supra-orbital processes absent	Vespertilionidae
Premaxilla present as a thin bone bearing a large incisor on each side with a wide space between them; frontals hollowed; cranium very large and high above the muzzle; no supra-orbital processes	Molossidae

Chiroptera genera			
Molossidae: *Sauromys*	Muzzle broad, level with flattened cranium	Premaxilla divided anteriorly	One small alveolus for anterior premolar; one incisor alveolus
Molossidae: *Tadarida*	Muzzle broad, level with somewhat flattened cranium	Premaxilla divided anteriorly	One moderate-sized alveolus for anterior premolar; one incisor alveolus
Vespertilionidae: *Miniopterus*	Frontal greatly enlarged above level of muzzle	Premaxilla divided anteriorly	Two alveoli for anterior premolar; two incisor alveoli
Vespertilionidae: *Neoromicia*	Muzzle broad, level with cranium (cf *Eptesicus* but smaller; width across M^2 5.3–6.0 mm; Roberts (1951))	Premaxilla divided anteriorly	No anterior premolar; two incisor alveoli, central larger than lateral
Vespertilionidae: *Cistugo*	Frontal slightly raised	Premaxilla divided anteriorly	Two minute anterior premolar alveoli transverse to toothrow; two incisor alveoli
Vespertilionidae: *Eptesicus*	Muzzle broad, level with cranium (cf *Neoromicia* but larger; width across M^2 8.1–9.0 mm; Roberts (1951))	Premaxilla divided anteriorly	No anterior premolar; two incisor alveoli, central larger than lateral
Nycteridae:	Broad flat plates expanding outwards above orbits, leaving a deep hollow between;	Premaxilla a thin plate with two wide vacuities in nasal region (normally missing)	No anterior premolar; two incisor alveoli
Rhinolophidae: *Rhinolophus*	Frontal bulbous; interorbital region very constricted; median crest in larger species	Thin premaxilla normally missing, leaving deep emargination between maxillae	Alveolus of single very small anterior premolar on outer border of toothrow; one incisor

Appendix 3

Features used to distinguish mandibles of Wonderwerk micromammals in the absence of diagnostic teeth. Numbers of teeth or alveoli refer to half (left or right) mandibles. See Roberts (1951) for further measurements, and text for further discussion.

Orders		
	Diastema between incisors and cheekteeth	Rodentia
	No diastema between incisors and cheekteeth	2
2	Coronoid process triangular; six or seven teeth; anterior incisor large & procumbent	Eulipotyphla: Soricidae
	Coronoid process broader than high; nine or 10 teeth, all single-rooted; M_3 greatly reduced or missing; anterior teeth not enlarged	Afrosoricida: Chrysochloridae
	Coronoid process higher than broad; five anterior teeth single-rooted, posterior five double-rooted; anterior teeth small	Macroscelidea: Macroscelididae
	Coronoid process variable but generally low; orthodont canines moderately enlarged	Chiroptera

(*continued on next page*)

Appendix 3 (*continued*)

Rodentia families		
1	Three cheekteeth (alveoli thereof), one incisor	Muridae
	Four cheekteeth (alveoli thereof), one incisor	2
2	Larger (combined length of cheekteeth alveoli ± 4.8 mm in *C. hottentotus*); ascending ramus very stout; incisor alveolus prominent	Bathyergidae: *Cryptomys*
	Smaller (combined length of cheekteeth alveoli ± 3.8 mm in *G. murinus*); ascending ramus not stout; incisor alveolus not prominent	Myoxidae: *Graphiurus*

Muridae sub-families & genera		
1	M_1 with multiple alveoli	Otomyinae: *Otomys*
	M_1 with four or fewer alveoli	2
3	Muscle attachment pronounced in region of mental foramen	4
	Muscle attachment not pronounced in region of mental foramen	6
4	M_1 with four alveoli	5
	M_1 with three alveoli	Gerbillinae: *Desmodillus*
5	Large (anterior–posterior length of M_1 alveoli ± 3.6 mm)	Gerbillinae: *Tatera*
	Small (anterior–posterior length of M_1 alveoli ± 2.3 mm)	Gerbillinae: *Gerbillurus*
6	M_1 usually with four alveoli	7
	M_1 with two alveoli	10
7	Large (anterior–posterior length of M_1 alveoli ± 3.2 mm)	Murinae: *Dasymys*
	Large-medium (anterior–posterior length of M_1 alveoli ± 2.5 mm)	8
	Small-medium (anterior–posterior length of M_1 alveoli ≥ 2.1 mm)	9
8	M_2 with three alveoli (M_1 with three alveoli in some species)	Murinae: *Aethomys*
	M_2 with five or six alveoli	Murinae: *Lemniscomys*
9	M_2 with four alveoli	Murinae: *Thallomys*
	M_2 with three alveoli	Murinae: *Rhabdomys*
10	Muscle attachment contiguous with mental foramen	11
	Muscle attachment not contiguous with mental foramen	12
11	Small (anterior–posterior length of M_1 alveoli ± 1.4 mm)	Petromyscinae: *Petromyscus*
	Large-medium (anterior–posterior length of M_1 alveoli ± 2.4 mm); alveoli tending to be round	Murinae: *Zelotomys*
	Small-medium (anterior–posterior length of M_1 alveoli ± 2.2 mm); alveoli narrower anterior–posteriorly	Murinae: *Mastomys*
12	Muscle attachment reaching level of M_1 anterior root; M_3 two- or three-rooted	13
	Muscle attachment not reaching level of M_1 anterior root; M_3 much reduced and single-rooted	14
13	Large (anterior–posterior length of M_1 alveoli ± 3.5 mm); M_1 alveoli widely separated	Mystromyinae: *Mystromys*
	Medium (anterior–posterior length of M_1 alveoli ± 2.6 mm); mandibular corpus relatively deep	Cricetomyinae: *Saccostomus*
	Small (anterior–posterior length of M_1 alveoli ± 1.5 mm); M_3 generally three-rooted	Murinae: *Mus*
14	Muscle attachment reaching beyond level of M_1 posterior root	15
	Muscle attachment not reaching beyond level of M_1 posterior root	Dendromurinae: *Malacothrix*
15	Larger (anterior–posterior length of M_1 alveoli ± 1.8 mm)	Dendromurinae: *Steatomys*
	Smaller (anterior–posterior length of M_1 alveoli > 1.5 mm)	Dendromurinae: *Dendromus*

Eulipotyphla (Soricidae)		
1	Articular surface of condyle approximates a right-angled triangle; posterior border of condyle nearly vertical in buccal aspect; coronoid spicule directed more or less posteriorly; P_4 bicuspate	*Myosorex*
	Articular surface of condyle approximates an isosceles triangle; posterior border of condyle slopes upwards and outwards in buccal aspect; coronoid spicule more or less directed vertically; P_4 unicuspate	2
2	Generally larger (molar alveoli ± 3.6 mm in medium-sized *C. cyanea*)	*Crocidura*
	Generally smaller (molar alveoli ± 1.8 mm in largest species, *S. varilla*)	*Suncus*

Afrosoricida (Chrysochloridae)	
Larger (total alveolar length ± 14.2 mm in *C. trevelyani*); border between coronoid process & condyle concave; angular process sickle shaped	*Chrysospalax*
Smaller (total alveolar length ± 7.8 mm); border between coronoid process & condyle not concave; angular process squared	*Chlorotalpa*

Macroscelidea (Macroscelididae)	
Adult mandible relatively short and lower margin markedly convex; inferior border of angular process angled; mandibular foramen smaller and set above level of superior margin of mandible	*Macroscelides*
Adult mandible relatively long and lower margin less markedly convex; inferior border of angular process curved; mandibular foramen larger and set level with or above superior margin of mandible	*Elephantulus*

Chiroptera genera			
Molossidae: *Sauromys*	Inferior border flat below toothrow but rising slightly below ascending ramus	Coronoid process pointed triangular	Two small anterior & two larger posterior premolar alveoli; anterior alveolus outside toothrow; two incisor alveoli
Molossidae: *Tadarida*	Inferior border flat below toothrow but rising slightly below ascending ramus	Coronoid process pointed triangular	Four premolar alveoli in toothrow; two incisor alveoli

Appendix 3 (*continued*)

Chiroptera genera			
Vespertilionidae: *Miniopterus*	Inferior border flat below toothrow but rising sharply below ascending ramus	Condyle & coronoid process level; anterior border of coronoid process vertical; angular process level with superior mandibular border	Five premolar alveoli; three incisor alveoli
Vespertilionidae: *Neoromicia*	Inferior border sloping upwards from symphysis; symphysis sloping about 45°	Coronoid process well developed, rounded; angular process level with superior mandibular border	Three premolar alveoli; three incisor alveoli
Vespertilionidae: *Cistugo*	Inferior border flat below toothrow but rising below ascending ramus	Coronoid process pointed triangular; anterior border vertical; angular process at level of superior mandibular border	Two small anterior & two larger posterior premolar alveoli; two incisor alveoli
Vespertilionidae: *Eptesicus*	Mandibular border flat below toothrow but rising slightly below ascending ramus	Coronoid process well developed, rounded equilateral triangular	Three premolar alveoli; two incisor alveoli
Nycteridae: *Nycteris*	Inferior border flat, parallel with superior border; symphysis nearly vertical	Small pointed equilateral triangular coronoid process; angular process vestigial	Three premolar alveoli, posterior greatly reduced; three incisor alveoli
Rhinolophidae: *Rhinolophus*	Inferior border flat below toothrow but rising below ascending ramus; symphysis nearly vertical	Very small coronoid process; angular process level with inferior border of mandible	Four premolar alveoli; very small second alveolus either in or outside toothrow; three incisor alveoli

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